

V1. *On the Formation of some of the Subaxial Arches in Man.* By GEORGE W. CALLENDER, *Assistant-Surgeon to and Lecturer on Anatomy at St. Bartholomew's Hospital.* Communicated by J. PAGET, F.R.S.

Received February 17,—Read March 16, 1871.

IN a previous communication on the formation of the bones of the face*, I described the manner in which the nasal and incisor processes of the maxillary lobes united with the fronto-nasal process, and the way in which the intermaxillary bones were shut off from the front surface of the face. I also described the ossification of the membrane which surrounds the anterior portion of MECKEL'S cartilage on either side, and that of the anterior and mesial extremities of the cartilages themselves. I now propose to examine the formation of the arches below these structures, commencing with that commonly known as the hyoid.

To simplify the grouping of these several arches I propose to term them subaxial. The first of the subaxial arches is the fronto-nasal, the basis of which is formed by the trabeculæ cranii. I take the notochord as the central line around which the development of the cerebro-spinal axis progresses. Now the trabeculæ, at first two separate cartilage-rods, grow out beneath (in man in front of) the extremity of the notochord. After the fusion of the trabeculæ their double origin is indicated by the median septum growing from their under surface. They inclose, by being prolonged forwards and downwards, the nasal passages, and they end in the intermaxillary bones. They are therefore subaxial in relation to the notochord, and conform generally to the plan on which the other subaxial arches are developed, the modifications which distinguish them being due to their terminal position, to the tubular shape of the long nasal passages which they have to form, and to the support which they give to those outgrowths from the cerebral vesicles, the olfactory bulbs and the front portions of the cerebral hemispheres.

The second subaxial arch grows from the lower and outer part of the alæ of the sphenoid, and is the one usually described as the maxillary; it is said not to contain cartilage. The third subaxial arch is the mandibular; it is strengthened by rods of cartilage (MECKEL'S) growing from that in which the internal ear is developed. Of other points in the formation of this arch, and of the connexions of the fourth arch with the cartilage of the internal ear, I hope to give an account when I have examined the various steps in the formation and growth of the cartilaginous base of the skull. At present it was convenient to pass them by until I had dissected the structures in the cervical region.

* Philosophical Transactions, 1869, p. 163.

The subaxial arches below the mandibular are the fourth, or lingual; the fifth, or hyoid; the sixth, or laryngeal; and the seventh, which, differing from the preceding in its relation to the notochord, may be named the exoccipital or shoulder-girdle. There is also an imperfect arch connected with the laryngeal which will be described with it.

The changes which will be described as occurring in the formation of these structures take place between the fifth and twelfth weeks of foetal life (30th to 84th day)*.

The Fourth Subaxial Arch—the Lingual.

In a foetus less than $\cdot 4$ of an inch in length this arch is recognized as a small bud-like process below the mandibular†; in a foetus measuring $\cdot 45$ this bud has grown out to the middle line, and has joined its fellow below the mandible (Plate I. fig. 1, *l*). The mandible, rather less than $\cdot 18$ from side to side and $\cdot 03$ deep, is yet membranous, and is closely connected by its lower border with the lingual arch; but in the midst of the connecting membrane two distinct lines of dense tissue are distinctly traced, meeting in the middle line. On either side of this they swell up into a pointed mass, and here the tongue is rapidly formed; so rapidly, indeed, that whilst in a foetus of $\cdot 45$ its position is indicated only by an ill-defined thickening of the tissue above the centre of the arch, in another foetus of $\cdot 55$ it is seen completely formed. From the eighth to the ninth week (foetus $\cdot 9$) the lingual arch, distinct from the hyoid, grows into a rounded cord which begins to contain cartilage. It is attached by a globular head to the cartilage for the internal ear below and behind the root of MECKEL'S cartilage; its anterior extremity descends to the next lower arch, becomes slightly swollen, and loses its distinct character in the structures passing into the base of the tongue; so that in a foetus of $1\cdot 2$ this extremity is no longer recognized, although the rising of its tissue into the root of the tongue is still traceable (Plate I. fig. 2, *l*, fig. 3, *l*). The lower border is now, by the anterior extremity, in close relationship with the upper surface of the hyoid and contains cartilage, the future lesser horn of the hyoid bone.

At this stage, ninth to tenth week, the connexion of this arch with the cartilage at the base of the skull is as follows: the globular head is still distinct, and seems partially cut off from the basal cartilage (Plate I. fig. 3, *ll*). From this point, for $\cdot 05$ of an inch forward, the rod is formed of cartilage; the remainder ($\cdot 07$ long), except the extreme anterior portion already spoken of, is a dense membrane. In the opposite direction (Plate I. fig. 3, *ll* to *lll*) there is continued from the rod a ridge of membrane, lying on and becoming identified with the cartilage of the base; and this, after ascending for $\cdot 05$ of an inch, turns forward and is continuous with membrane, a descending spur from which forms a distinct ring, which extends to that in which the squamous and zygomatic bones are ossified, and which appears to be continued into the membrane in front of MECKEL'S cartilage (Plate I. fig. 3, *mc*), now ossified as the inferior maxilla (Plate I.

* The specimens on which the dissections were made are in the Museum of St. Bartholomew's Hospital. The figures indicating the size of each foetus give its length in inches and tenths of an inch.

† Here and after the relations are given as for human anatomy.

fig. 3, *m*) or mandible: MECKEL'S cartilage is seen growing out beneath the membrane and then passing under cover of the lower jaw.

In a foetus 1·8 long, tenth to eleventh week, the lingual arch consists of five portions,—(1) cartilage from the base of the skull, (2) a short piece of membrane, (3) a second very small and short rod of cartilage, these three structures having a length of ·09 of an inch (Plate I. fig 5, *l* to *l**), (4) a long strip of membrane, and (5) a nodule of cartilage at the anterior extremity of the arch, which is connected with the hyoid below. The entire length of these structures is ·19 of an inch.

The Fifth Subaxial Arch—The Hyoid.

On a deeper plane and under cover of the parts in which the lingual arch is formed, a layer of membrane, comparatively broad, is seen growing out from the base of the skull in connexion with that part in which the basioccipital ossification takes place. In a foetus ·45 long it has the form shown in Plate I. fig. 1. This mass widens as it descends into the cervical region and towards the middle line, and divides into two chief parts; the higher of these is the hyoid arch.

This arch is at first represented by the upper portion of the layer of membrane, and by a bud of this membrane from the upper and mesial extremity of either side piece (Plate I. fig. 1, *h*). These buds meet in the middle line and there unite, so that in a foetus ·9 long they form a distinct rod, now cartilaginous as far back as the point *h**, fig. 2, rather less than ·1 of an inch long, where it is connected with the mass of membrane continued down to the larynx. The band of tissue connecting this arch with the thyroid cartilage at the point *h**, fig. 2, is now just discernible; in the next dissection, that of a foetus 1·2, it is distinctly formed. The higher portion of this arch, towards the base of the skull, forms the middle constrictor muscle, which in a foetus 1·8 can be traced from the base into the posterior portion of the cartilage of the arch, the greater or posterior horn of the hyoid bone.

The posterior portion of this arch, therefore, is membranous, and develops into the middle constrictor muscle; the cartilage in the anterior two-thirds (·06 long in a foetus of ·9, and 1·1 in a foetus of 1·8) consists of two portions, the one the greater horn, the other the body of the hyoid bone.

The Sixth Subaxial Arch—The Laryngeal.

Whilst the upper portion of the layer of membrane from the basioccipital cartilage grows forward to form the hyoid arch, the lower division, first distinctly separated from the upper by anterior bud-like outgrowths, forms a mass in the cervical region which in a foetus of ·45 is about ·05 of an inch in length (Plate I. fig. 1, *lg*). This mass, uniting with a corresponding growth from the opposite side, forms an irregular line in the middle of the neck, all trace of which line rapidly disappears. At first it lies flat upon the vertebræ, but quickly thickens, and in a foetus ·9 forms a thick block advanced to the level of the anterior extremity of the lingual arch (Plate I. fig. 2, *th*, *cr*). As it thickens

and rises to the front, a passage is left behind it leading from the mouth to the œsophagus, and common to the pharynx and to the larynx.

At this period the membrane consists of three layers. The inner of these folds in and forms a septum, which divides the larynx from the common pharyngeal tube, and growing up below the root of the tongue forms the epiglottis. These growths are completed in a foetus $\cdot 9$ of an inch long. The outer layer is that in which the constrictor muscles originate, whilst in the anterior portion of the arch there is an intermediate or third layer of dense granular and subsequently cartilaginous tissue, in which are formed the several cartilages of the larynx, excepting the epiglottis.

The upper portion of this arch, therefore, forms the inferior constrictor muscles, and at this early period of development blends with that tissue in which the middle constrictor of either side is developed (Plate I. figs. 3, 4, 5). The remainder of the arch becomes, like the hyoid, cartilaginous in the greater part of its extent. In a foetus $\cdot 9$ the outline of the thyroid cartilage is distinct, and also that of the front and sides of the cricoid, but posteriorly the horns of the thyroid are imperfectly recognized, the upper one not being as yet cartilaginous, whilst the arytenoid and cricoid cartilages are not yet completely separated from the thyroid behind (Plate I. fig. 2, *th*, *cr*, *ar*).

Thus far these structures whilst bent over towards the middle line are on either side perfectly flat, and altogether form a mass $\cdot 06$ long and $\cdot 05$ wide. Their continuity with the pharyngeal wall is easily traced.

In a foetus $1\cdot 2$ the separation of the principal cartilages is complete and the cornua of the thyroid are formed (Plate I. fig. 3, *th*, *cr*, *ar*). Although the first granular masses of cartilage appear in the thyroid and in the fore part of the cricoid, yet the chondrification of the membrane extends so rapidly to the posterior parts of the cricoid and to the arytenoid, that no practical distinction can be made between the times of these quickly consecutive changes.

The next step in the development of this arch consists in the curving of the cricoid and arytenoid cartilages into the septum which separates the larynx from the pharynx. In a foetus $1\cdot 4$ (Plate I. fig. 4, larynx $\cdot 9$ long and $\cdot 1$ wide) the turning in of these structures towards the middle line is evident; and in a foetus $1\cdot 8$ (Plate I. fig. 5, larynx $\cdot 12$ long and $\cdot 12$ wide) is being completed. At this stage I notice a narrow edge of membrane turning down from the greater horn of the hyoid arch, and joining the inner and upper surface of the arytenoid cartilage (Plate I. fig. 5). The appearances of the fissures marking the divisions between the laryngeal cartilages are drawn in figs. 2, 3, 4, & 5.

The Thyroid Body.

The external part of the lower half of the laryngeal arch developes into an accessory structure, the thyroid body. From the seventh to the ninth week it may be recognized as a distinct mass, having the characters which I have described in a previous communication*; it lies by the side of the arytenoid and cricoid cartilages, from which it can easily

* Proceedings of the Royal Society, vol. xvi. p. 183.

be detached, and grows downwards and forwards to meet the corresponding structure from the opposite side in the middle line (Plate I. fig. 2, fig. 3, *th. b*). Although it is difficult to assign to it any particular function, it may be noticed that it is in relation with the respiratory tract in its development, and is virtually a rudimentary branchial arch*; and further, that it forms a girdle beneath which the air-tube is continued, and perhaps guided, as the trachea into the thorax.

The Trachea.

Whilst the cartilages of the larynx are acquiring their permanent characters, the trachea is formed by a continuous growth from the membrane below the cricoid cartilage. I have not as yet definitely traced out the formation of the bronchi; there is, I believe, no doubt but that they result from the division of the trachea.

The Seventh or Exoccipital Arch—The Shoulder-girdle.

At first it occurred to me that this should be termed a subaxial arch, and it still seems desirable to number it as following the sixth or laryngeal outgrowth of membrane from the base of the skull. But exception might be taken to the term subaxial, as defined to refer to the position of an arch with reference to the notochord, when applied to this structure; for the membrane from which the clavicle and scapula take origin grows out from the cartilage of the base of the skull in a line from the extremity of the membrane for the hyoid and laryngeal arches, below the lingual arch, and all along the side and hind plate in which the exoccipital and supraoccipital ossifications commence. From these the membrane of this arch is separated with some difficulty, leaving a rough edge. Thus whilst the membrane for the hyoid and laryngeal arches grows from the basioccipital region and is subaxial, that for the shoulder-girdle extends from the lateral and posterior portions of the occipital cartilage, having also for a short distance relations with the cartilage for the structures connected with the internal ear; it therefore is best described as an exoccipital arch, growing from the cartilage of the base of the skull, but at the side of and behind the axis line represented by the notochord.

The growth of this membrane is extremely simple. Dissecting at about the thirty-fifth day (foetus .45), it is seen as a fold of membrane extending from the root of the mandible on either side downwards, its connexion with the mandible being formed by

* With reference to this point I would refer to the remarks which I made when examining the relations of this body. "One cannot but be attracted by this connexion with the trachea, on which tube the thyroid (even if it be not developed from the membranous air-tube) buds and attains some little size, a formation reminding one of that of the lungs coming out from the front wall of the œsophagus, that is, from the trachea, and of the view of Mr. SIMON, as afterwards expressed by the editors of CUVIER respecting the thyroid, 'C'est la fausse branchie, branchiole des poissons.' Indeed, from its relation to the air-tube during the early period of life, or in fish to the vertebral or hyoid extremity of the gill, from its curious alternation with the supplementary gill of Broussonet, and from its structure (Kölliker), it may be not inaptly referred to as a pseudo-lung rather than as an associate with the thymus and the so-called ductless glands."—Proceedings of the Royal Society, vol. xvi. p. 185.

the integumental covering. If this fold is everted, a band of tissue can be traced to an angle above, where it comes into contact with the well-defined tissue in which the larynx is to be formed (Plate I. fig. 6). On the inner surface of the fold two ridges (Plate I. fig. 6, *c*, *s*) are imperfectly marked, but at the lower end of the membrane they are more distinct,—one ending in a rounded border (and here the clavicle is developed), the other, which lies behind the first, descending a little lower and being slightly bent with the convexity of the curve backwards (in this the scapula is formed).

In a foetus more advanced ($\cdot 55$), after removal of the integument and of the upper thoracic extremity, the plate of membrane is more clearly defined. It grows from the occipital region, and above is in close relationship with the membrane for the laryngeal arch (Plate I. fig. 7). Traced downwards, it sends forward a comparatively delicate layer of tissue (Plate I. fig. 7, *c*), which extends to the superior extremity of that (*st*) in which the sternum and the costal cartilages are being formed. At about the middle of the lowest border of the arch a rounded mass, which is granular, and in which cartilage is appearing, forms a considerable elevation (*s*), pushed forward as it is by the ribs which have now grown up beneath it (*r*). This rod is curved, as shown in fig. 7; its superior and anterior extremity is the acromion, its inferior extremity is the coracoid process; and nearly midway between the two a bud-like outgrowth (which seems to originate in a folding over of the integument), the thoracic extremity, has been removed in the specimen from which the drawing (fig. 7) was made.

The changes thus far related consist in the division of the membrane growing out from the occipital region into two portions, the anterior of which develops into the hyoid and laryngeal arches, whilst the posterior division descends and forms a broad layer in the neck (covered by integument), which eventually forms the sterno-mastoid and trapezius muscles of either side, and behind joins above in the middle line the tissue from the opposite side at the ligamentum nuchæ: below it sends out two processes; one of these grows forward to form the clavicle and to join the sternum, the other curves downwards and forms the scapula, and from this there grows out the thoracic extremity.

It will be noticed that these outgrowths, including the lingual, correspond not inexactly with the course of the cerebral nerves distributed below the mandible,—(1) the hypoglossal, (2) the glossopharyngeal, (3) the pneumogastric, and (4) the spinal accessory.

In a foetus $\cdot 9$ long the clavicle has ossified in its middle third, the remainder is cartilaginous; it is $\cdot 09$ of an inch long. When the ossification of this bone is described as taking place in membrane, it is to be understood that only the earliest formed portion of the bone is so ossified; the greater part of the clavicle, about two-thirds of its length, ossifies in cartilage, which rapidly takes the place of the original membrane, and of which only small plates are left at either end of the bone in a foetus $1\cdot 2$ (in Plate I. figs. 8 and 9, the earliest membrane ossification and the extension of the ossification in cartilage are shown).

By the growth of the sternum to the middle line and by the attachment to it of the

clavicle, which is also connected with the first rib, the anterior portion of the seventh arch is brought from an oblique into a line nearly horizontal (in Man), and at this period the portion of membrane above it, which at first lies close along the upper border of the clavicle, becomes detached from the outer half of this border, or is united only by a thin layer of tissue. The tissue which remains connected with the inner half, or thereabouts, of the clavicle forms the sterno-mastoid muscle.

The inner extremity (Plate I. fig. 7, *a*) of the rod of cartilage (which is the scapula) being connected with the outer extremity of the clavicle is brought into the same horizontal line with that bone and forms the acromion. The coracoid extremity of the scapula (Plate I. fig. 7 and following, *co*) becomes more curved upon the acromial, to the level of which it eventually reaches (chiefly by the straightening in a downward direction of the acromion), and thus the entire scapula forms a slightly spiral curve, and the root of the coracoid portion becomes attached to the clavicle by a strong fibrous band. In this spiral curving of the rod of cartilage which forms the scapula the upper surface of the coracoid corresponds with the upper surface, its internal surface with the anterior, and its external with the posterior border of the acromion process. By the same curving of this portion of the arch the lower portion of the posterior border of the membrane ascending to the occipital region is bent or folded inwards; and this seems to explain the connexions acquired by the levator anguli scapulæ muscle in the cervical region, and its insertion into the end of the plate of the scapula which grows from the root of the coracoid process.

The growth of the plates of the scapula takes place from the posterior border of the rod of cartilage, the form of the bone being determined by the curve of the primitive rod. Following the posterior border the acromion plate is seen (fig. 8, *a*) growing backwards, whilst from the remainder of the rod to the root of the coracoid the larger plate bounded by the glenoid border is developed. Scarcely any growth has yet taken place from the coracoid (fig. 8, *co*), but in a foetus 1·2 (fig. 9, *co*) it is beginning to throw out its plate, and in a foetus 1·8 (fig. 10, *co. p*) this plate is being rapidly completed. The scapula is thus built up in the three-sided prismatic form referred to by Professor FLOWER*.

Later, comparatively, in the formation of the scapula (foetus 1·8, fig. 10) the glenoid cavity grows out from the rest of the cartilage, and thus leaves a considerable notch between it and the acromion, and the scapula now acquires its permanent characters.

Up to this point no ossification is observable, nor have I recognized any segmentation of the primitive rod. When ossification commences it begins, as shown by Mr. PARKER, in the central portion of the rod, as is the case with the clavicle, and, as with the clavicle, it leaves two cartilage ends, which are the acromion and the coracoid process.

* Osteology of the Mammalia, p. 334.

EXPLANATION OF THE PLATE.

PLATE I.

- Fig. 1. Subaxial and exoccipital arches in a foetus ($\cdot 45$ of an inch long). $\times 6$.
- Fig. 2. Lingual, hyoid, and laryngeal arches, with the thyroid body, in a foetus $\cdot 9$ of an inch long. $\times 6$.
- Fig. 3. The same arches as in fig. 2, with the addition of the mandibular. The divisions of the hyoid and laryngeal arches are shown, and also the connexion of the lingual arch with cartilage and membrane at the base and side of the skull. From a foetus $1\cdot 2$ of an inch long. $\times 6$.
- Fig. 4. The same arches at a more advanced stage, from a foetus $1\cdot 4$ of an inch long. $\times 6$. The anterior portion of the lingual arch has been removed.
- Fig. 5. The same structures, including the lingual arch, in a foetus $1\cdot 8$ of an inch long. $\times 6$.
- Fig. 6. Ridges seen on the inner surface of the exoccipital arch in a foetus $\cdot 45$ of an inch long. $\times 6$.
- Fig. 7. Outer surface of the exoccipital arch, showing the division of its lower border into the clavicular and scapular rods, and the growth beneath these of the sternum and ribs. From a foetus $\cdot 55$ of an inch long. $\times 6$.
- Fig. 8. Dorsal and ventral surfaces of the scapula of a foetus $\cdot 9$ of an inch long. $\times 6$.
- Fig. 9. The same surfaces of the scapula of a foetus $1\cdot 2$ of an inch long. In this and in the preceding figure the anterior surface of the clavicle is also represented. $\times 6$.
- Fig. 10. Dorsal surface of the scapula of a foetus $1\cdot 8$ of an inch long, showing the outgrowth of the glenoid cavity and of the coracoid plate. $\times 6$.

EXPLANATION OF ABBREVIATIONS.

- a.* Acromion.
- ar.* Arytenoid cartilage.
- c.* Clavicle.
- cm.* Constrictor muscles of pharynx.
- co.* Coracoid process.
- co. p.* Coracoid plate of scapula.
- cr.* Cricoid cartilage.
- g.* Glenoid cavity and border.
- h.* Hyoid arch.
- h*.* Posterior extremity of the cartilage of the hyoid arch.

- l.* Lingual arch.
- ll.* Basal extremity, or head, of lingual arch.
- lll.* Membrane connected with basal extremity of lingual arch.
- l**. Second cartilage of lingual arch.
- lg.* Laryngeal arch.
- m.* Mandible.
- m c.* MECKEL'S cartilage.
- r.* Ribs.
- s.* Scapula.
- st.* Sternum.
- th.* Thyroid cartilage.
- th. b.* Thyroid body.

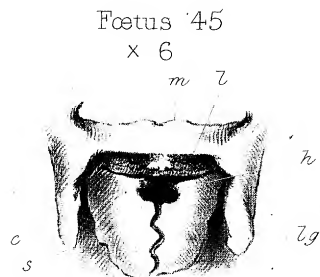


Fig I.

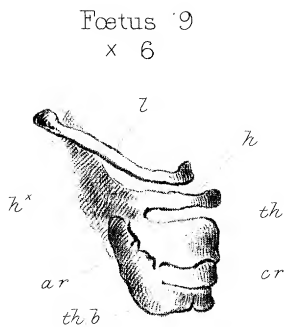


Fig II.

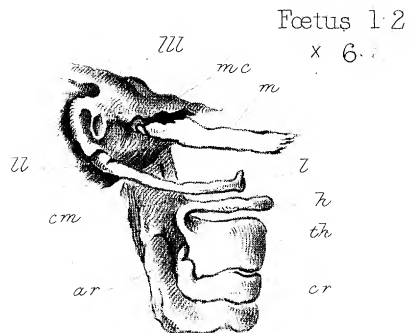


Fig III.

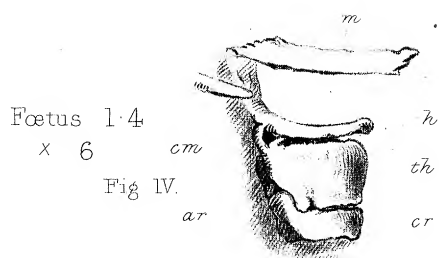


Fig IV.

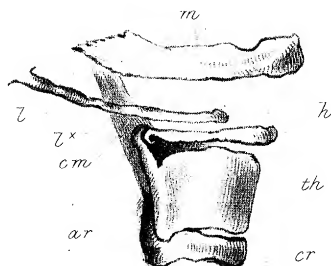


Fig V.

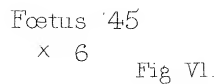


Fig VI.

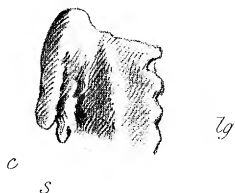
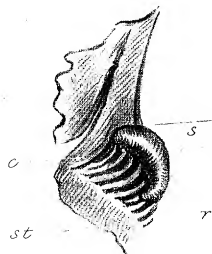
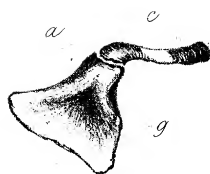


Fig VII.



Foetus 55
x 6

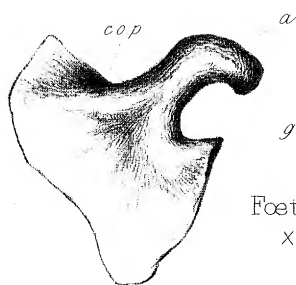


Foetus 9
x 6

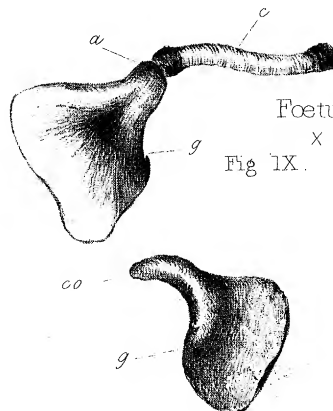
Fig VIII.



Fig IX.



Foetus 1.8
x 6



Foetus 1.2
x 6

Fig IX.